

Patterns of Radular Tooth Structure in Carnivorous Land Snails ¹

BY

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(7 Plates)

INTRODUCTION

IN A MAGNIFICENT ANALYTIC paper, WATSON (1915) demonstrated the multiple origin of carnivores among land snails and outlined the basic modifications required in their evolution. In a concluding section, WATSON (1915, pp. 254-256) suggested a classification of the carnivorous taxa that has been little modified by subsequent work. Because the convergences produced by adoption of a carnivorous diet are so striking, it still is uncertain as to how the families that are strictly carnivorous are related to herbivorous taxa. ZILCH (1959-1960, pp. 543-555), for example, grouped the Systrophiidae, Haplotrematidae, Rhytididae, Aperidae, and Streptaxidae together in the Streptaxacea. Slightly earlier, H. B. BAKER (1956) had suggested that the Systrophiidae might be a family of the Limacacea; Streptaxidae a family of the Achatinoidea lineage; Oleacinidae a member of the Oleacinoidea; while the Aperidae, Rhytididae, and Haplotrematidae were grouped together as the Rhytidoidea. Subsequently BAKER (1962a, 1962b, 1963) refined this system and expanded it, grouping the Sagdidae and Oleacinidae as a superfamily Oleacinaea in the Holopoda, placing the Testacellidae and Systrophiidae in the Aulacopoda, and distributing the other families among the Holopodopes as follows: Spiraxidae in the Achatinacea; Streptaxidae in a superfamily by itself; the Haplotrematidae, Rhytididae, Aperidae, and restricted Acaavidae in the Rhytidacea.

The present paper does not consider the correctness of these allocations, but is concerned solely with the diversity of radular modifications. WATSON (1915: 228-229) had outlined five major changes in radular structure.

These may be paraphrased as: 1) The entire radula is enlarged, lengthened, and capable of far greater protrusion from the mouth; 2) individual teeth, particularly those equivalent in position to the mammalian canines, will be greatly enlarged, while those in the central and outer portions of the radula will be reduced in size; 3) the mesoconal cusps will be longer and more sharply pointed, the secondary cusps generally are absent, and there is no distinction between lateral and marginal teeth; 4) the basal plates of the teeth will be lengthened to prevent the teeth from being bent outwards; and 5) the transverse rows of teeth will be sharply angled in the center of the radula. Comments on these aspects will be deferred until after the discussion of individual species.

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MATERIALS AND METHODS

Specimens available in the collections of Field Museum of Natural History (hereafter FMNH) and an example of *Prolesophanta dyeri* (Petterd, 1879) from the National Museum of Victoria, Melbourne, Australia were used for this initial survey. The species illustrated are:

STREPTAXIDAE

Restartemon aff. *colombianus* (Pilsbry, 1935)

FMNH 168006 from Socorpa Mission, 1 300-1 400 meters elevation, Sierra de Perija, Magdalena, Colombia (9°45'N; 73° 20'W). Borys Malkin! August 1968.

Oophana diaphanoepepla van Benthem Jutting, 1954

FMNH 147666. South face of Bukit Serdam, near Raub, Malaya. Barbara Solem! April 21, 1962.

RHYTIDIDAE

Torresiropa gradata (Gould, 1846)

FMNH 153057. Sta. 10, Togotigiga, 15m elevation, Upolu, Western Samoa. A. Solem and L. Price! November 2, 1965

Prolesophanta dyeri (Petterd, 1879)

National Museum of Victoria. Badger Creek, below Corran-derk Weir, Victoria, Australia. D. C. Long! November 30, 1969.

Ptychorhytida aulacospira (Pfeiffer, 1846)

FMNH 159351. Top of Col de Momen, near Moindou, mid-west coast of New Caledonia. L. Price! November 11, 1967.

Diplomphalus seberti (Marie, 1881)

FMNH 158375. Sta. 19, Dethio-Nakety Road, summit of di- vide, 360 m elevation, New Caledonia. L. Price! October 22, 1967.

HAPLOTREMATIDAE

Haplotrema minimum (Ancey, 1888)

FMNH 98105. East end of Berkeley Tunnel, Alameda Co., California. A. Solem and A. Smith! April 9, 1960.

SYSTROPHIIDAE

Systrophia eudiscus H. B. Baker, 1925

FMNH 167951. Sierra de Perija foothills, 200-300 m elevation, El Rincon, east of Becerril, Dept. Cesar, Colombia. Borys Malkin! September 16-22, 1969.

OLEACINIDAE

Euglandina rosea (Férussac, 1821)

Daytona Beach, Florida. A deceased pet named "Wolfe," un-catalogued.

The above nine taxa belong to 5 of the 8 carnivorous land snail families of the Stylommatophora. Only the South African Aperidae, European Testacellidae, and the Neotropical Spiraxidae are omitted. The other carnivorous family, the Rathousiidae, from the Malay Peninsula and Indonesia, is a member of the Systellommatophora, not the Stylommatophora. Their inclusion would have increased the taxa surveyed, but not changed the basic conclusion of diversity in radular patterns.

Specimens were prepared for scanning electron microscope (hereafter SEM) observation by the technique outlined in SOLEM (1972). References to other radular studies using the SEM are given in SOLEM (1972, 1973) and are not repeated here.

OBSERVATIONS

The individual discussions are designed to answer two questions concerning radular functioning. First, how does the tooth function and how is it supported during the stress of cutting into its prey, and second, how are the teeth compactly folded when not raised in a feeding stroke.

In earlier reports (SOLEM, 1972, 1973) I have shown that longitudinal interrow support during feeding stroke stress is widely developed among pulmonates. Convergent patterns of cusp structure can be recognized as such by diver-

Explanation of Figures 1 to 6

Euglandina rosea (Férussac, 1821)

Figures 1-3: Daytona Beach, Florida. Figure 1: radular teeth in folded position at 270X. Figure 2: detail of folded middle teeth at 850X. Figure 3: teeth raised for a slicing stroke at 880X.

Haplotrema minimum (Ancey, 1888)

Figures 4-6: south side of road, east end of Berkeley Tunnel, Alameda Co., California. A. Solem & A. Smith. April 9, 1960. Field Museum of Natural History number 98105. Figure 4: partial row viewed from posterior at 365X. Figure 5: elevated and bent teeth at 410X. Figure 6: marginal teeth showing basal support at 1000X.



gent interrow support systems (SOLEM, 1973) and in some taxa such as the Partulidae, there is a separate support pattern among the marginal teeth of the same row (SOLEM, 1973: fig. 19). The lateral teeth and central tooth in both Partulidae (SOLEM, 1973: figs. 13, 15, 18, 20, 21) and Enidae (SOLEM, 1973: fig. 7) have broadly overlapping row to row support, while in groups such as the Camaeniidae (SOLEM, 1972), the overlap is narrower and highly varied. Subsequent observations (SOLEM, unpublished) have confirmed the presence of an interrow support system in many other families. Alteration or loss of this interrow support system in carnivorous taxa was a primary subject for investigation. It is absent in all examined taxa, with an odontophoral cartilage-tooth support system substituted.

The other major query concerns how the teeth can be compactly folded when not functioning in feeding. Not only must the more posterior teeth be kept folded, but with their increased size and length, avoidance of any damage to the mouth interior would require effective tooth folding and compaction. The species discussions do not follow phyletic order, but are presented according to type of structure and illustration order.

Euglandina rosea (Férussac, 1821)

When folded (Figure 1) the acute angulation of the tooth rows is obvious. The reduced central tooth lies under the broadly overlapping lateromarginals (Figure 2). There is little radical change in tooth size, only a gradual decrease from center to outer margin. The teeth fold inward against the side of the next inner tooth, with tip curved free (Figure 2) of the shaft. When elevated (Figure 3), their appearance is drastically altered. Each tooth is an elevated slicer, with its anterior margin sharply truncated. When under full stress, this relatively broad anterior margin can be appressed against the basal membrane and its underlying cartilage to provide a buttressed support against the stress of feeding. A semiligament, visible in upper portions of Figure 3, acts to aid the downward fold of the tooth.

These teeth function as blade-like slicers, depending on a truncated anterior margin for support during extreme stress of feeding. The folding pattern is simple and the change in tooth size, except for the reduced central, is gradual and even from center to outer margin of the radula.

Haplotrema minimum (Ancey, 1888)

The outermost teeth (Figure 6) are small, elongated, and curved, with a distinct anterior support prolongation that

is attached for its entire length. Viewed above from a relatively high angle, the size increase from outer margin (Figure 4 left) to midsection is rapid and accelerating. For the larger, more central teeth (Figure 4 right) the blade becomes thicker, more curved, the anterior (top) elongation relatively shorter and with its tip free of the basal membrane. Seen directly from above (Figure 5 left) the midrange teeth are extremely narrow blades that can be quite readily compacted by folding inward on top of the next tooth towards the row center. As the larger inner teeth are reached, there is a distinct shape change (Figures 4, 12). The blade becomes higher, convex on the outer and concave on the inner margin. This has two effects, turning the tip into a "trowel-like" point (Figure 12), and providing a positive interlock system for the folded teeth.

In function, the outer teeth appear simple slicers, but the larger inner teeth combine aspects of stabbing and slicing with a variable tension anterior support. Because of their curved anterior tip to the support structure, the larger teeth can "give" substantially under cutting stress, yet continue to receive support from the underlying cartilage as the tooth is further bent from the "normal" elevated plane. The curved short anterior base of the inner teeth provides support at several angles for heavy cutting work, while the elongated fixed basal support of the outer teeth provides firm support for their accessory cutting work. While basically remaining as simple "slicers," the changed shape of the inner teeth, with (Figure 12) their tips pointed forward, thus combines "stabbing" and "slicing" aspects.

Systrophia eudiscus H. B. Baker, 1925

The outermost teeth (Figure 7) are shorter and stubbier than in *Haplotrema*, the anterior (right) basal support is higher, completely attached, and there is a slight posterior (left) extension to the basal plate. Viewed from an outside angle (Figure 9), the outer teeth are seen to become more elongated, elevated at a sharper angle, and with the anterior basal extension (right side) tending to truncate and become free of attachment. Teeth from the same zone of the radula viewed from an inside angle (Figure 8, lower left) show the truncated free tip, and also (lower center) demonstrate the presence of a lateral, inner indentation on each cusp that effectively permits compacted folding of the teeth towards the center. This rather shallow grooving functions because of the sharply angled placement of adjacent teeth (Figures 10, 11). When the more central teeth are viewed from above (Figure 11) and then at a posterior angle of the bent radula (upper right of Figure 11), the narrow tip of the big cutting teeth (compare with Figure 12 of *Haplotrema*), the broadened shaft of the cusp com-

pared with *Euglandina* (Figure 3), and the sharper angulation of the row compared with *Haplotrema* (Figures 4, 5), but not *Euglandina* (Figures 1, 2), are obvious. A simulated "feeding stroke" area was obtained only of worn teeth at the anterior tip of the radula (Figure 10). The blunted cusp tips are obvious, but the significant fact in this picture is the use of the truncated anterior support (center and lower right) as a stress support system. The free tip is still slightly curved, but much less than in *Haplotrema* (Figure 4). It thus is intermediate in character between *Haplotrema* and *Euglandina* (Figure 3).

In functioning, the outer teeth and the inner teeth of *Systrophia* combine aspects of "stabbing" and "slicing." The lower angle and broadened shaft of the cusp tend towards a "stab and spread" method of attack, but the degree of elevation obtainable by the inner teeth (Figure 10) and their narrow under edge suggest use in slicing as well.

Ptychorhynchida aulacospira (Pfeiffer, 1846)

Viewed in whole row aspect (Figure 16), the great reduction in number of teeth and the changed pattern of relative tooth size are obvious. The center area teeth (Figure 17) are vestigial, reduced to low and elongated form. There is sudden and rapid size increase culminating in two very large teeth, followed by a single somewhat smaller outermost tooth. This is the classic tooth pattern postulated by WATSON (1915). Seen from posterior view (Figure 13) and in twisted position from above (Figure 15), the "stab and tear" cusp structure is obvious. Viewed at a low angle from the radula center outwards (Figure 14), the grooved inner sides of the cusp and base indicate effective compacted folding. The elongated nature of the teeth and completely attached anterior extension show that these teeth must be used strictly in a "stab and tear"

Explanation of Figures 7 to 12

Systrophia eudiscus H. B. Baker, 1925

Figures 7-11: Sierra de Perija foothills, 200-300 m elevation, El Rincon, east of Becerril, Dept. Cesar, Colombia. Borys Malkin. September 16-22, 1969. Field Museum of Natural History number 167951. Figure 7: detail of outer marginals at 1380X. Figure 8: middle teeth at 725X. Figure 9: part row of teeth at 505X. Figure 10: elevated, worn teeth showing basal support at 470X. Figure 11: posterior angle view of elevated teeth at 1000X.

Haplotrema minimum (Ancey, 1888)

Figure 12: same data as Figures 4-5: posterior angle view of elevated cusps at 895X.

function. The cusps retain a slender shape (Figure 15) and would not tend to "spread" open the cut as much as in the cutting action of *Haplotrema* (Figure 12) or *Systrophia* (Figure 11).

The functioning position of these teeth is at a low angle to "stab and tear," while the deeply grooved inner surface of the cusps and bases (Figure 14) show how tightly compacted folding can be accomplished. It is quite possible that the interlock from tooth to tooth might be used to provide a single massive functional cutting surface (see Figures 15, 16, 17) during a feeding stroke. Investigation of the actual feeding position will be possible with critical point drying of the buccal mass and study of the anterior teeth on the odontophoral cartilages, but use of this technique has not been possible to date.

Unintentional mounting of a severely deformed radula (Figures 18-21) enabled seeing what great damage can result without preventing effective feeding. The left side of the radula (Figure 19, left) has only one functional tooth (Figure 21, right side), with the other big teeth fused into an amorphous, non-elevated mass (Figure 19, left center). On the right side (Figures 18, 19, 20), the main teeth have fused into a bifurcated massive structure that is well elevated (Figure 20). The outermost right side tooth is reduced to a narrow curved strip, while the innermost (Figure 20, right) of the normal four big teeth (Figure 15) is a short stubby hooked remnant. The entire radula showed this deformity, so it was of significant duration in time and

Explanation of Figures 13 to 17

Ptychorhynchida aulacospira (Pfeiffer, 1846)

Top of Col de Momen, near Moindou, midwest coast of New Caledonia. Laurie Price. November 11, 1967. Field Museum of Natural History number 159351. Figure 13: posterior angle view of elevated middle teeth at 485X. Figure 14: lateral view of elevated middle teeth at 162X. Figure 15: view of twisted and normal positioned outer teeth at 213X. Figure 16: partial row of teeth from above at 93X. Figure 17: half row of teeth from above at 210X.

Explanation of Figures 18 to 21

Ptychorhynchida aulacospira (Pfeiffer, 1846)

Same data as for Figures 13-17. Figure 18: top view of deformed major teeth at 225X. Figure 19: top view of deformed part row at 165X. Figure 20: side view of deformed tooth from center of radula at 575X. Figure 21: deformed part row of teeth at 190X.



